

The Circadian Rhythm of Oviposition in *Drosophila melanogaster*: A Genetic Latitudinal Cline in Wild Populations

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(1976)

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Summary. Under laboratory conditions with a photoperiod of 12 h at a light intensity of about 1100 lux, *Drosophila melanogaster* strains of different latitudinal origin showed significant differences in oviposition rhythm. These genetic differences follow a cline and may have an adaptative value.

Behavioural genetic variations are probably of great importance in evolutionary processes^{2,3}. Such changes may be significant for the initiation of sexual isolation and also for the diversification into ecological niches.

In *Drosophila*, oviposition rhythm is a convenient trait for characterizing one behavioural aspect of species or populations⁴. Oviposition recordings can be easily made on an hourly basis and give highly reproducible results: the average curve, typical of a given strain, is reproduced almost exactly in successive and independent experiments⁵.

Previous works^{6,7} have demonstrated that *D. melanogaster* wild populations exhibit genetic latitudinal clines for certain biometrical traits (adult fresh weight and

female ovariole number) and for a physiological trait, alcohol tolerance. Since behavioural differences are probably more directly linked to fitness, we decided to

¹ We thank F. AYALA, R. GRANTHAM and D. LEWONTIN for help with the manuscript.

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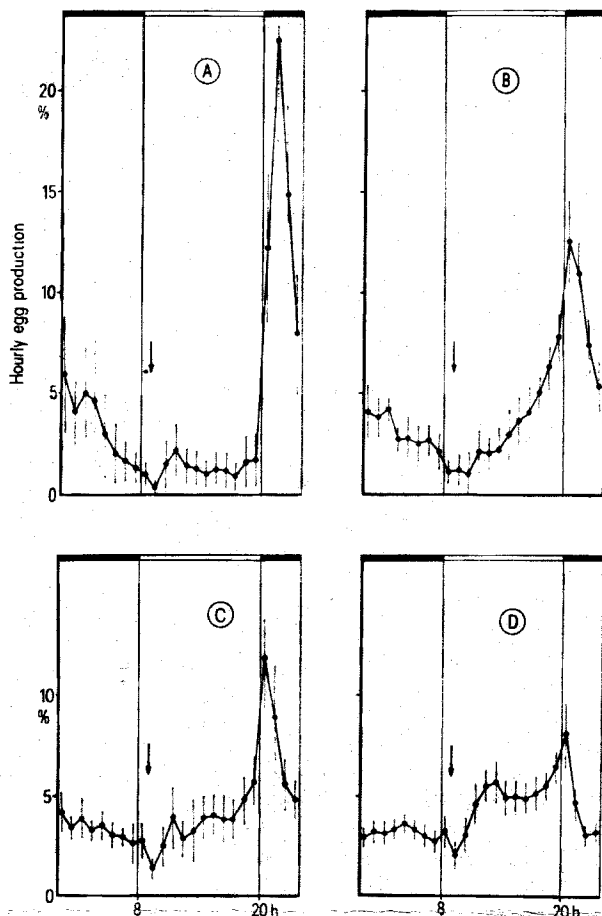


Fig. 1. Examples of oviposition curves of wild strains from different origins. Strains from A) Agboville (Ivory coast); B) Ouarzazate (Morocco); C) Sammeron (France); D) Helsinki (Finland). Heavy and light horizontal bars indicate the photoperiodic cycle (LD 12:12). Hourly data are expressed in percent of the daily egg production; vertical lines around each point indicate the confidence intervals; arrows point to the time of changing the food medium (see ref. ⁵ for further information on methods). Each curve was established from several repetitions (A) 10; B) 13; C) 12; D) 25) and usually corresponds to a total oviposition of more than 3000 eggs.

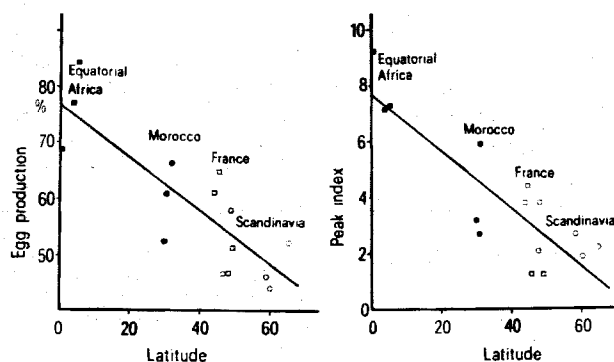


Fig. 2. Variations in oviposition rhythm with latitude of strain origin. A) percent of daily egg production during the 12 h of photophase; B) peak index, ratio of peak height to width. In both cases, a linear regression can be fitted to the observed points and the decrease with latitude is highly significant (A) $r = -0.82$, $p < 0.001$; B) $r = -0.86$, $p < 0.001$).

analyze the oviposition rhythm in 15 strains from Africa and Europe. Latitudes of origin of the strains ranged from 0° (Equator) to above 60° (Northern Europe). The longitudes were between 25° East and 10° West. For each strain, several repeated measurements (often more than 15) were made and an average curve was calculated. 4 examples of such curves are given in Figure 1.

Under the experimental conditions chosen (LD 12:12 cycle, light intensity about 1100 lux) egg laying is always at a low level during the photophase with a peak at the beginning of the scotophase. However, significant differences exist between the strains, with respect to the anticipation of the peak during the photophase and mainly the height of the peak. For an overall comparison of the 15 strains, two traits were chosen: the proportion of the eggs laid during the photophase and an index which characterizes peak size (ratio of height to width). Within each strain, these traits are correlated ($r = 0.85$) and, when plotted against the latitude of strain origin, they give similar results (Figure 2).

In both cases, a decrease with latitude is observed. 80% of the daily egg production in strains from equatorial countries is laid during the 12 h of darkness and the oviposition peak is about 8 times higher than it is wide. In strains from Scandinavia, females lay a little less than 50% of their eggs during darkness and the peak index is only about 2.

Since the experiments were made on strains reared under the same laboratory conditions, the differences described must have a genetic basis. In some cases, crosses were made between different strains and the curves for the F_1 offspring appeared intermediate between those of their parents. Usually, the measurements were made on strains recently collected from wild populations. Measurements were repeated in some strains after 1 or 2 years of laboratory rearing and these gave curves very similar to the initial ones. These observations suggest that several loci are involved in the genetic determinism of the rhythm. The apparent absence of genetic drift under laboratory conditions might be explained by a nearly homozygous state of the strains.

As emphasized in previous reports^{6,7}, regular latitudinal clines for a genetically based variation demonstrate the adaptative value of the trait and also may give an indication on the nature of the environmental factors which selected the wild populations. For example, an increase in size with latitude in *Drosophila* can be explained by a better tolerance to cold or to various environmental stresses^{8,9}. An increase in alcohol tolerance can be interpreted as a modification of feeding habits⁷. The data presented here suggest that natural selection, which is probably responsible for any latitudinal cline, can modify a behavioural trait. Some preliminary experiments indicate that oviposition rhythm could depend on light intensity. For example, an equatorial strain laid more eggs during the photophase when the light intensity was lowered. The oviposition difference could thus be related to differences in light sensitivity. If such is the case, our results would have some similarities with variations in photopathic reaction previously described in *D. melanogaster*¹⁰.

The latitudinal clines described in Figure 2 can be correlated with climatic conditions of the countries of origin. A significant correlation ($r = -0.70$, $p < 0.01$) was found with the amplitude of variations in day length in

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summer. No significant correlations were found, however, either with the number of hours of sunshine during the year or with the light energy received at the earth surface. Of course, since temperature is strongly influenced by latitude, a positive correlation is also observed between the rhythm and the average annual temperature ($r = 0.75$) or the amplitude of thermal variations ($r = -0.84$). The adaptive significance of our data therefore cannot be ascertained with certitude. There is now increasing evidence that the whole *melanogaster* subgroup, and *D. melanogaster* itself, originated in tropical Africa¹¹. We can therefore suppose that the rhythm tended to disappear as the geographic range extended northward. Flies establishing colonies in areas where the light conditions change considerably during the year became less sensitive to, or less dependent on, environmental light.

Much attention has recently been paid to the genetic polymorphism of wild populations and to the possible adaptive importance of oligogenic biochemical variants¹². Some indications now exist that structural genes are not only the source of evolutionary changes, and that variations at the level of regulatory DNA should also be considered^{13,14}. Polygenic traits, the genetic molecular basis of which remains unclear, could prove to be more interesting than previously believed.

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¹³ M. C. KING and A. C. WILSON, Science 188, 107 (1975).

¹⁴ G. B. KOLATA, Science 189, 446 (1975).